

BIOLOGICAL AND ROBOTIC MODELING OF THE EVOLUTION OF LEGGED LOCOMOTION ON LAND

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BIOLOGICAL AND ROBOTIC MODELING OF THE EVOLUTION OF LEGGED LOCOMOTION ON LAND

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SUMMARY

In the evolutionary transition from aquatic to terrestrial environments, early walkers adapted to the challenges of locomotion on complex, flowable substrates (e.g. sand and mud). Our previous biological and robotic studies have demonstrated that locomotion on such substrates is sensitive to both limb morphology and kinematics. Although reconstructions of early vertebrate skeletal morphologies exist, the kinematic strategies required for successful locomotion by these organisms have not yet been explored. To gain insight into how early walkers contended with complex substrates, we developed a robotic model with appendage morphology inspired by a model analog organism, the mudskipper (*Oxuderichinae*). We tested mudskippers and the robot on different substrates, including rigid ground and dry granular media, varying incline angle. The mudskippers moved effectively on all level substrates using a fin-driven gait. But as incline angle increased, the animals used their tails in concert with their fins to generate propulsion. Adding an actuated tail to the robot improved robustness, making possible locomotion on otherwise inaccessible inclines. With these discoveries, we are elucidating a minimal template that may have allowed the early walkers to adapt to locomotion on land.

CHAPTER I

INTRODUCTION

Throughout history, many organisms have used flipper-like limbs for both aquatic and terrestrial locomotion. Modern examples include mudskippers and sea turtles; extinct examples include early walkers such as *Acanthostega* and *Tiktaalik*. Among the many adaptations made by flipper-driven vertebrates in evolutionary history, perhaps the most significant was the first transition made by early walkers from an aquatic to a terrestrial environment, commonly referred to as the invasion of land. In making this transition, early vertebrates contended with many biomechanical and substrate interaction challenges. In particular, they moved on flowable ground, such as sand and mud, using a flipper-like appendage that could be planted in the substrate. These substrates present a significant challenge because they exhibit complex rheology, and can both jam like a solid or yield and flow like a fluid. Recent reconstructions of fossilized early walkers, such as that of *Ichthyostega* [2], can provide information about the possible ranges of motion of limbs. However, how limb-joint morphology couples with limb kinematics to produce locomotion in complex environments has not yet been elucidated. Previous work [3] has shown that identical morphologies can result in dramatically different locomotor performance on complex substrates when kinematics are varied. While many studies have addressed morphological differences among early walkers to speculate on locomotor efficacy [4], this observation suggests kinematics also play a crucial role. Potential insight to be gained from computational modelling of flipper-substrate interaction dynamics is constrained by the lack of a theoretical understanding of the physics of complex, flowable substrates. For example, while the Jenkins-Richmann equations provide a theory for granular gas like phases

[5], there are no known general constituent equations for granular materials (in the regimes in which we are interested) as there are for fluids (i.e. Navier Stokes), and models are thus restricted to coarse grained approximations, such as low Reynolds number fluid simulations and resistive force theory. However, these models do not account for emergent substrate dynamics intrinsic to complex materials, which have been shown to influence organism locomotion strategies in nontrivial ways [3]. Previous work combining biological and robotic modelling of organismal locomotion has proven to be fruitful in elucidating the physical mechanisms by which organisms interact and adapt to their environments. For example, a study by Mazouchova et. al. revealed the importance of a flexible wrist for flipper driven locomotion in both live hatchling sea turtles and a sea-turtle inspired robot, a result related to the jamming of substrate material behind and beneath the flipper [3].

To gain insight into the morphological and kinematic principles that may have facilitated the invasion of land, we employed a combined biological and robotic approach to the study of flipper driven locomotion. We studied the crutching gait of an extant model analog organism for early terrestrial locomotion, the mudskipper, in a variety of wet and dry granular substrates, and developed a physical robot model based on the morphological features of the reconstructed early walkers, and the kinematic parameters of the mudskippers. The robotic model allowed for precise variation of kinematic parameters, such as flipper insertion depth and presentation angle. Furthermore, we studied its locomotion on inclined granular substrates in order to gain insight into robustness of kinematic configurations. These experiments have begun to reveal a minimal feature set necessary for robust terrestrial locomotion with minimal control.

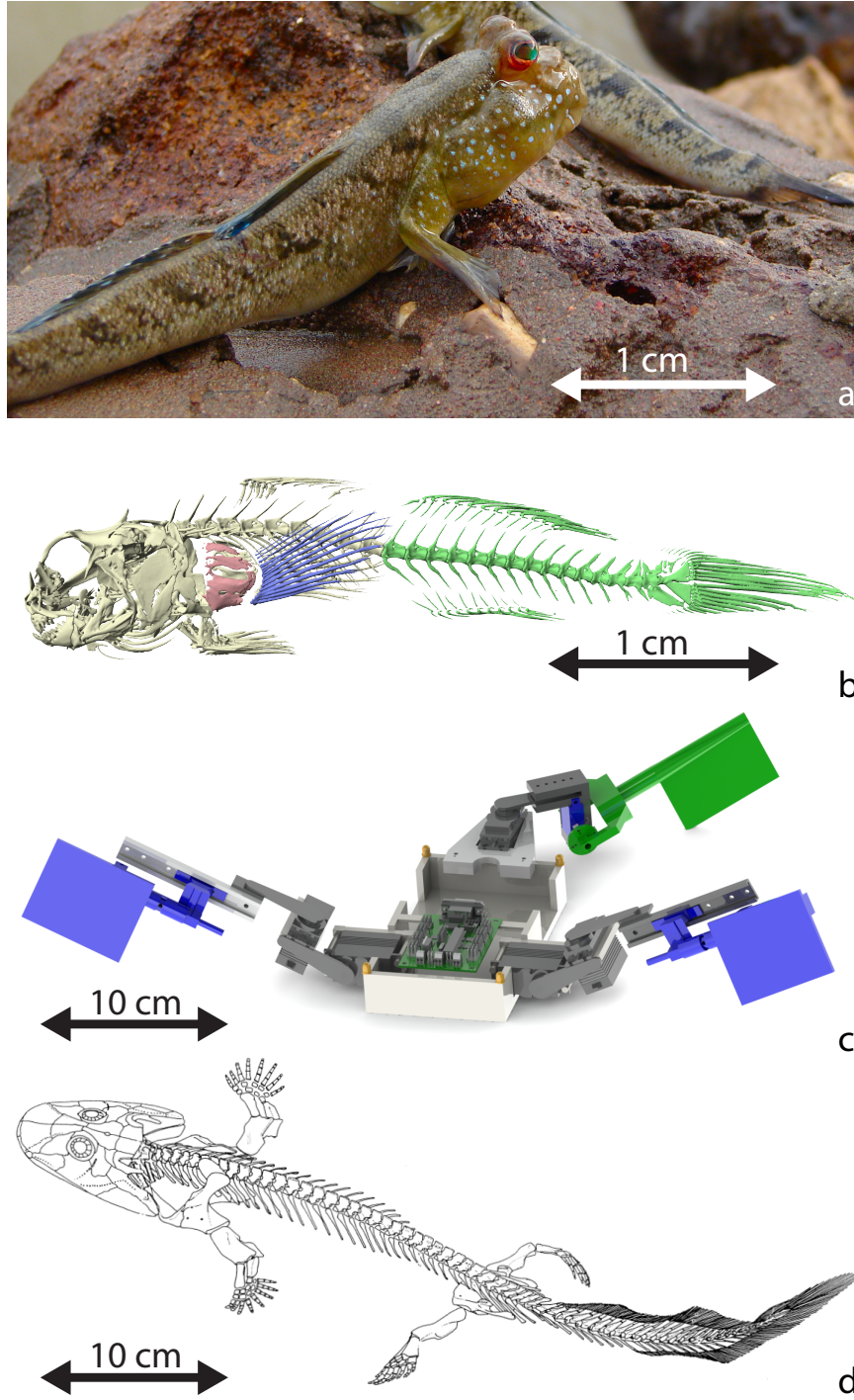


Figure 1: (a) The mudskipper (*Periophthalmus barbarus*), a model organism for early terrestrial walkers (CT scan). (b) The MuddyBot, a 3D printed robot developed to study the evolution of legged locomotion. (c) Skeletal reconstruction of *Acanthostega gunnari* (figure reproduced with permission from Michael Coates [1]).

CHAPTER II

LITERATURE REVIEW

Throughout history, many organisms have used flipper-like limbs for both aquatic and terrestrial locomotion. Modern examples include mudskippers and sea turtles; extinct examples include early walkers such as *Acanthostega* and *Tiktaalik*. Among the many adaptations made by flipper-driven vertebrates in evolutionary history, perhaps the most significant was the first transition made by early walkers from an aquatic to a terrestrial environment, commonly referred to as the invasion of land. This adaptation necessitated changes to limb morphology and kinematics in order to overcome the challenges flowable terrestrial media, such as sand and mud, pose to terrestrial locomotion. While great efforts have been made to understand the body plans of these early walkers [1], the physical principles underlying how they were able to invade land have not yet been elucidated. Previous studies, using both physical robotic models [6] and live organisms [7], have revealed the high sensitivity of locomotor efficacy to both limb morphology and kinematics on flowable substrates[6]. For example, Li et. al. found that a small shift in the limb phase of a hexapedal robot determined whether it was able to move effectively on a granular substrate, where the optimal limb cycle for hard ground locomotion resulted in failure. From such results, it is clear that early vertebrates were forced to adapt not only the shapes and structures of their limbs, but also how they used them, in order to make themselves robust to complex substrates and environments. Recent work in paleontology has revealed the limb-joint skeletal morphology of early walkers, such as *Ichthyostega* [2], in remarkable detail. However, the role of limb kinematics in the invasion of land, and particularly the importance of the vertebrate tail, has not yet been explored,

despite the presence of developed, seemingly muscular tails in early vertebrates such as *Acanthostega*, and the likelihood that these tails were used for both swimming and locomotion at the bottom of ponds [1].

The use of robotic physical models has proved to be an invaluable tool for gaining insight into the physical principles of organismal locomotion on flowable substrates [7]. Complex materials such as sand and mud lack constituent equations analogous to the Navier-Stokes equation for fluids, limiting computational studies to resistive force theory approximations, which treat the media as a high Reynolds number fluid, and neglect emergent properties such as jamming, which can influence limb-media interaction in non-trivial ways [7]. Robotic models allow for precise manipulation of both morphological and kinematic parameters, and for reductions of parameter space to the biomechanical feature set under study. A previous study by Mazouchova et. al [3] discovered, using a robotic model, that the addition of a passive, flexible wrist to a flipper-based robot aided its locomotion over a granular substrate. This mechanism is related to the jamming of material behind and beneath the flipper, thus allowing the robot to keep its flippers planted throughout the limb cycle, and is also an observed behavior in live hatchling sea turtles. These results provide insight into a particular extant flipper driven organism, the sea turtle. However, the efficacy of the flipper driven robot under other morphological and kinematic variations is not revealed, and furthermore, the role of the tail present in early walkers such as *Acanthostega* [1] is not explored. Most previous studies of early vertebrate biomechanics have been limited to studies of extant model analogue organisms, such as in a recent study by Standen et. al, in which the possible importance of developmental plasticity in the origin of tetrapod limbs was discovered through studies of *Polypterus* fish [8]. The work by Pierce et. al. on *Ichthyostega* suggests that its mode of locomotion was most likely front-wheel driven, that is, the front limbs were the primary generators of thrust [2]. The proposed gait was probably similar to the crutching gait utilized by

the extant mudskipper fish (*Oxuderichinae*), an organism that has evolved for both effective aquatic and terrestrial locomotion. Kawano et. al recently discovered that hard-ground vertical ground reaction forces for mudskipper pectoral fins are relatively low, compared to those for digitated salamander limbs [9]. This result suggests that forelimbs may have played an important role in primitive terrestrial locomotion, as suggested by Pierce et. al [2], and provides further support for the mudskipper as a valid analogue for early vertebrates. However, the study did not include experiments of mudskipper locomotion on granular substrates, such as the sand early vertebrates had to traverse. As Li et. al. [6] demonstrated, the mechanics of limb-substrate interaction can vary dramatically between hard and flowable media, and it is not only possible that ground reaction forces differ on complex media, but also that flipper-driven locomotion alone as proposed by Pierce et. al [2]. may not actually be sufficient.

The present work will combine biological and robotic modeling of early vertebrate locomotion in order to elucidate a minimal feature set for robust terrestrial locomotion. We use mudskippers as a model analogue organism and observe their locomotion on dry and wet granular substrates at a variety of incline angles. Observations of mudskipper locomotion on natural substrates such as sand and mud provide more insight into the biomechanical and behavioral adaptations that may have facilitated early walker locomotion than previous hard-ground studies. We then develop a flipper-driven robot, the MuddyBot, to allow for systematic variation of important morphological and kinematic parameters observed in the mudskipper. In particular, we are able to not only vary the robots limb morphology to simulate an early tetrapods body plan, but from mudskipper experiments, are able to hypothesize and test potential locomotion gaits and limb cycles that may have allowed for early terrestrial locomotion. From these experiments, we discover that locomotion on granular inclines is dramatically different from locomotion on level substrates, in part due to

emergent material dynamics such as avalanching and jamming. We find that robust locomotion on granular inclines is not possible without use of the tail in addition to the forelimbs in both mudskippers and the robot, suggesting the appendage may be more important than previously expected. From this insight we develop a minimal control model for primitive, robust terrestrial locomotion.

CHAPTER III

METHODS AND PROCEDURES

3.1 Mudskipper Experiments

We chose to study the mudskipper fish (*Oxudericinae*, see Fig. 1a and Fig. 2) as a model organism for early vertebrates such as *Ichthyostega* and *Acanthostega*, as it employs a symmetric crutching gait hypothesized to be similar to the gait used by some early walkers [2]. Our collaborators, Dr. Sandy Kawano and Dr. Richard Blob, collected videos of the mudskippers' locomotion on both level and inclined dry, loose sand at Clemson University as a model for the substrates early walkers had to contend with during the invasion of land. Overhead and lateral high speed cameras recorded the motion of the fish in the granular media bed. To avoid bias in our results, experiments were performed using ten different individuals of the same species. We then analyzed the videos of the mudskippers' locomotion at Georgia Tech. For each video, the position of the fish in the bed over time was tracked and recorded using MATLAB-based tracking software [10]. Forward progress was measured as the forward displacement (Δx) of the mudskipper, the net displacement projected orthogonal to the axis of inclination of the trackway.

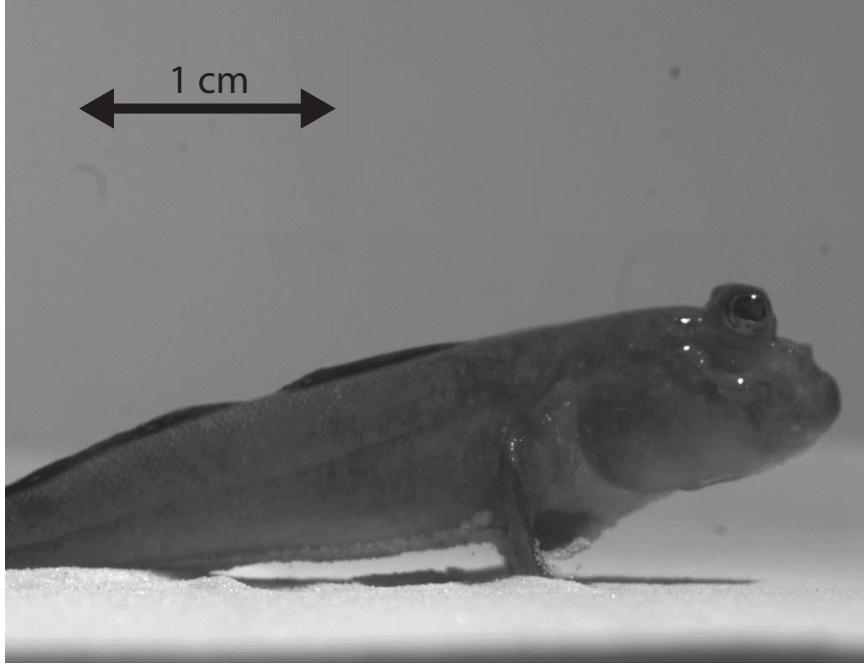


Figure 2: Lateral view of a mudskipper fish performing a crutching gait in a granular media bed filled with loose, dry sand. The fish were recorded with both lateral and overhead cameras to help reconstruct their trajectories in the bed.

3.2 Robot Experiments

To better understand the mechanisms behind flipper-driven locomotion on granular substrates, and to systematically vary locomotor features observed in the mudskippers, we developed a 3D printed flipper-driven robotic model inspired by the early walker morphology (Fig 1b, Fig. 3). The robot was actuated by two HiTec HS-M7990TH servos for each flipper, along with one HiTec HS-M7990TH servo and one HiTec HS-5055MG servo for the tail. In our experiments, we varied the supination angle (presentation angle of the flipper, held fixed throughout cycle), adduction angle (angle of flipper arm with respect to lateral body line of robot) of the robot’s flippers, and the robot’s tail use (Fig. 3). Control templates for tail use were designed based on three critical observations of the mudskippers. First, when the tail was not used

propulsively, it was lifted from the media to reduce drag. When the tail was used, the tail and flippers were never simultaneously raised from the media, and in the propulsive phase of the gait, the flippers and tail moved synchronously. When the tail was not used, the tail was lifted from the granular material. The robot experiments were performed on level and inclined substrates (Fig. 4), using two different types of dry granular substrate, poppy seeds (.3 mm radius) and plastic beads (3 mm radius), which in addition to having different material properties, are separated by an order of magnitude in length scale.

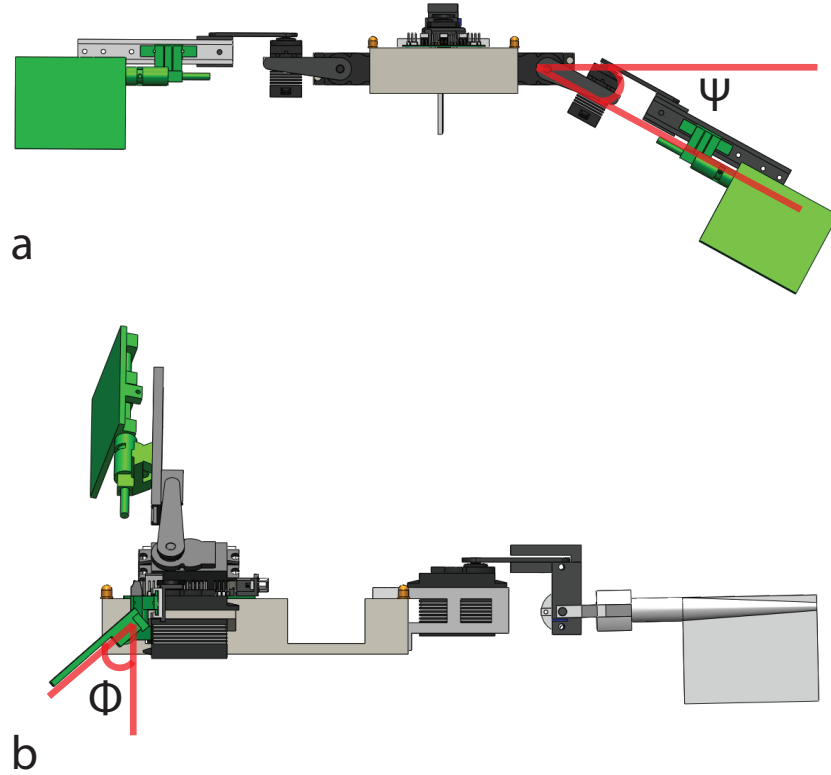


Figure 3: Varied parameters in the MuddyBot. (a) ψ , the adduction angle of the arm, was varied from -5° to 20° , in intervals of 5° . (b) ϕ , the supination angle of the flippers, was varied from -5° to 60° , in intervals of 15° . Both angles were held constant during the limb cycle.



Figure 4: The $1.23m$ by $1.83m$ bed used for robot experiments. Here the bed is filled with poppy seeds. For both poppy seeds and plastic beads, the bed was filled to a depth of 12 cm.

CHAPTER IV

RESULTS

4.1 Mudskipper Results

The mudskippers are capable of effective locomotion over level granular substrates using a forelimb-driven crutching gait alone, gaining an average Δx of 0.5 ± 0.1 body lengths with each limb cycle when the tail was not used, and 0.6 ± 0.1 body lengths when the tail is used (Fig. 5). However, as substrate incline angle increases to 10° and 20° , forelimb-driven crutching becomes less effective (Fig. 5). We further discovered that as incline angle of the media increased, the frequency of steps for which the tail was used propulsively increased, from 6.30% on level media to 32.9% on media inclined at 10° , to 46.2%, nearly half of all steps, on media inclined at 20° (Fig. 5).

Furthermore, as media angle increased, the disparity between forward displacement for steps in which the tail was used compared to those in which the tail was not used increased. At a 10° incline, an average of 0.4 ± 0.1 body lengths was gained with each step, compared to 0.5 ± 0.2 body lengths when the tail is used. When the media was inclined to 20° , steps for which the tail was not used achieved an average displacement of 0.2 ± 0.1 body lengths, less than half the displacement of steps for which the tail was used, 0.5 ± 0.2 body lengths.

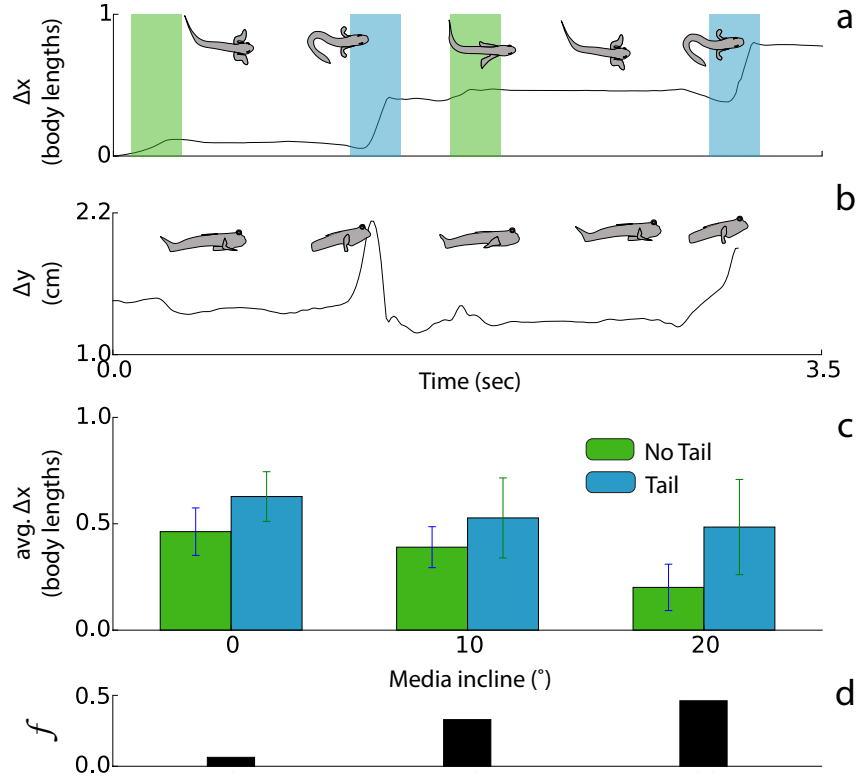


Figure 5: (a) Kinematics of the mudskipper fish on dry, loose sand inclined at 20°. Cycles without tail use are green regions, while cycles with tail use are indicated by blue regions, resulting in increased forward displacement per cycle (Δx). (b) Mudskipper lift height relative to media (Δy , measured from eye). Height increases during each step, with particular high lift coinciding with tail use. (c) As the incline angle of the media increases, average forward displacement per step declines more for steps in which the tail is not used than for steps in which the tail is used, indicating that tail use is increasingly necessary to the mudskippers as media incline angle increases. (d) Frequency of tail use (f) measured over all averaged steps. As media incline angle increases, the tail is used more frequently by the mudskippers.

4.2 *Robot Results*

To gain further insight into the mechanics of crutching locomotion on granular media, we varied the limb adduction angle, flipper supination angle, and tail use of the robot on two dry granular substrates, poppy seeds and plastic beads. The supination angle of the flippers was varied between 0° and 60° in 15° intervals. The adduction angle was varied between -5° and 20° in 5° intervals. The tail was either used or not used, and media incline angles of 0° , 10° , and 20° were used.

When the tail was not used, locomotion of the robot was robust on level media if the adduction angle of the flippers was sufficiently high (Fig. 6). However, when the media was inclined, for example to 20° (Fig. 6), the range of supination/adduction parameters for which locomotion was successful became increasingly limited to low supination and high adduction angles. When the tail was used, there was little to no effect on locomotor performance on level media (Fig. 6), but when the media was inclined, tail use substantially improved performance in almost all conditions, as well as allowing effective locomotion at combinations which result in total locomotor failure without tail use. In all cases, tail use induced alternating lateral rotations and displacements, which explain the few instances in which tail use was detrimental.

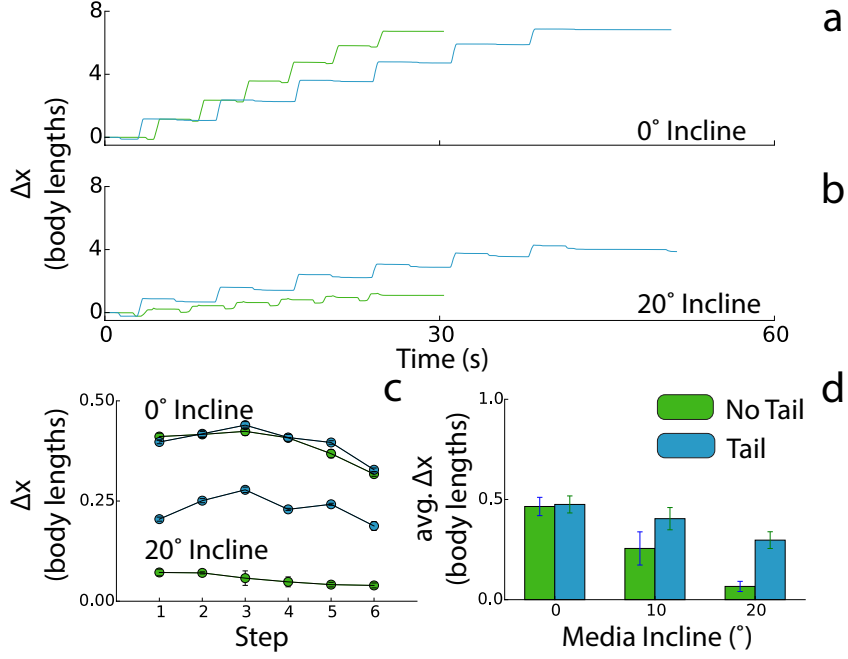


Figure 6: (a) Kinematics of a mudskippier inspired robot on level dry poppy seeds, with a supination angle (ϕ) of 15deg and an adduction angle (ψ) of 15deg. Green indicates no tail use, while blue indicates tail use. On level media, both net displacement and per step displacement are comparable. (b) Kinematics of robot on 20deg inclined poppy seeds with identical limb configuration as in (a). Δx decays more rapidly in the case for which the tail is not used, leading to significantly lower net displacement compared to the case in which the tail is used. (c) Δx for each step for experiments in (a) and (b). For level media, Δx is almost identical in each step for both tail use and no tail use cases, however, when the media is inclined, a significantly greater Δx is observed when the tail is used compared to when it is not used. (d) Δx , averaged over three experiments for with identical limb configuration for each incline angle. As with the mudskippers, as media incline angle increases, the improvement in Δx gained by using the tail increases.

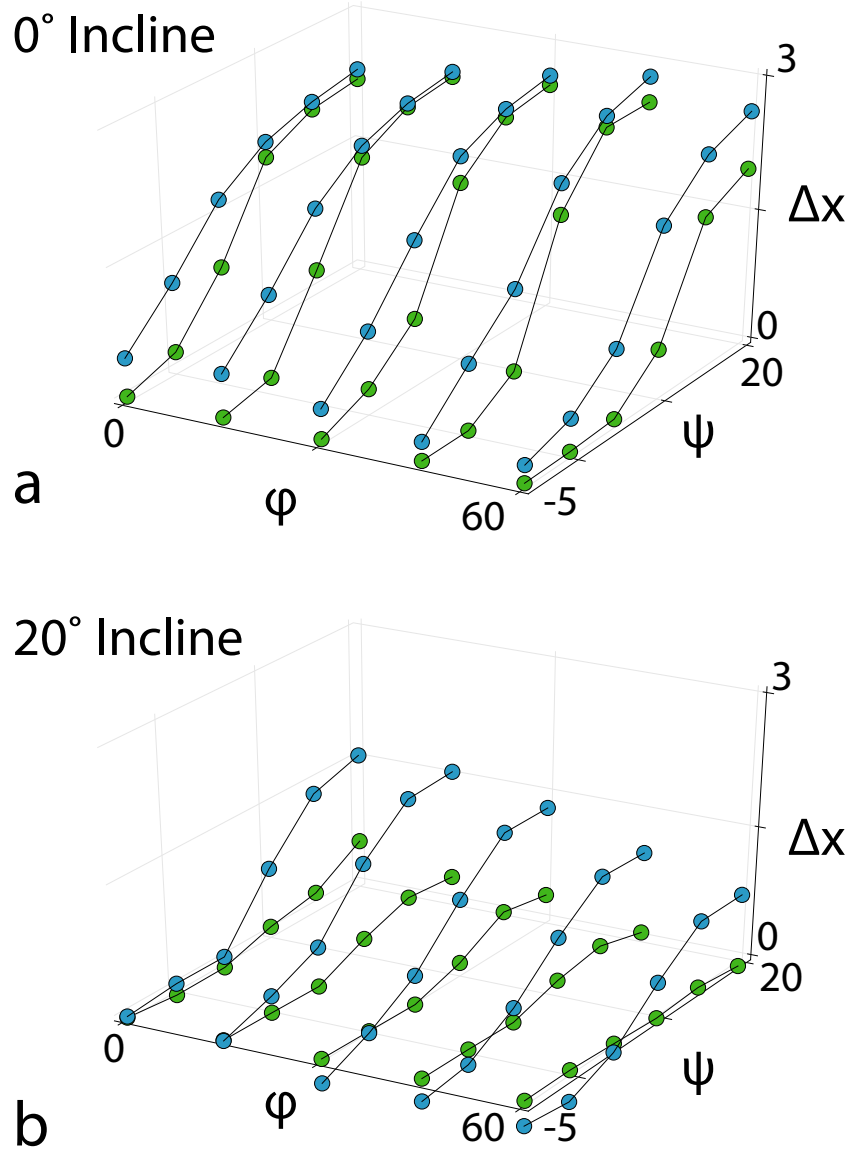


Figure 7: (a) Total forward displacement of the robot after six steps (Δx) on dry level poppy seeds, plotted against ϕ and ψ . Blue points indicate tail use, while green points indicate no tail use. Δx increases with increasing ψ . Tail use allows for some improvement at higher ϕ . (b) Δx on inclined dry poppy seeds. Increasing ψ again results in increased Δx . However, locomotor success only occurs for runs in which the tail is used.

CHAPTER V

DISCUSSION

We found that propulsive tail use aids the locomotion of both the mudskipper fish and a flipper driven robotic physical model, making both organism and robot robust to variations in media incline. However, even when the tail was used in the robot, successful locomotion was still only possible when the flippers were adducted to a sufficiently large angle. This result suggests that the 'push-up' motion, which was hypothesized to be important to the early walkers in the invasion of land and is observed in the mudskipper fish, is indeed a critical feature of robust terrestrial flipper-driven locomotion. Although use of the tail is not necessary for successful locomotion on level media, propulsive tail use allows the robot to move effectively on inclined media, with the range of successful supination/adduction configurations becoming increasingly limited as the media incline is increased.

CHAPTER VI

CONCLUSION

Employing a combined biological and robotic-physical approach, we have begun to elucidate a minimal locomotor apparatus for robust terrestrial locomotion. Our results suggest that while a strong shoulder girdle capable of allowing the early walkers to lift their bodies from the ground is a necessary feature for successful flipper-driven terrestrial locomotion, it is not sufficient to explain the robustness to variations in media incline that would have been critical to the early walkers' success. These early organisms exhibited strong tails, which until now have remained largely unexplored in the paleontological literature. By studying the locomotion of an extant model organism, the mudskipper fish, on inclined media, and developing a robotic physical model that allows for systematic variation of morphological and kinematic parameters. We discovered that the fish thrust their tails synchronously with their fins in order to push themselves upwards on inclined granular materials, with frequency of tail use increasing with media incline angle. Furthermore, we found that propulsive use of a simple tail dramatically improves the robot locomotion on inclines, making locomotion possible for limb configurations that otherwise would have failed, and thus effectively correcting for errors in limb placement.

CHAPTER VII

FUTURE WORK

The robotic model we have developed allows for systematic variation of both morphology and control. Future work will focus on coupling resistive force theory simulations with the robotic model to study how different control strategies and morphologies affect flipper driven locomotion. The simulations, based on geometric mechanics formalism, will allow us to search for optimal gaits in the space of internal degrees of freedom of the robot.

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Biological and Robotic Modeling of the Evolution of Legged Locomotion on Land

Benjamin W. McInroe

21 Pages

Directed by Professor Daniel I. Goldman

In the evolutionary transition from an aquatic to a terrestrial environment, early walkers adapted to the challenges of locomotion on complex, flowable substrates (e.g. sand and mud). Our previous biological and robotic studies have demonstrated that locomotion on such substrates is sensitive to both limb morphology and kinematics. Although reconstructions of early vertebrate skeletal morphologies exist, the kinematic strategies required for successful locomotion by these organisms have not yet been explored. To gain insight into how early walkers contended with complex substrates, we developed a robotic model with appendage morphology inspired by a model analog organism, the mudskipper. We tested mudskippers and the robot on different substrates, including rigid ground and dry granular media, varying incline angle. The mudskippers moved effectively on all level substrates using a fin-driven gait. But as incline angle increased, the animals used their tails in concert with their fins to generate propulsion. Adding an actuated tail to the robot improved robustness, making possible locomotion on otherwise inaccessible inclines. With these discoveries, we are elucidating a minimal template that may have allowed the early walkers to adapt to locomotion on land.